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DOI: https://doi.org/10.1523/JNEUROSCI.4089-09.2010

Behavioral/Systems/Cognitive

Value Computations in Ventral Medial Prefrontal Cortex during Charitable Decision Making Incorporate Input from Regions Involved in Social Cognition

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Little is known about the neural networks supporting value computation during complex social decisions. We investigated this question using functional magnetic resonance imaging while subjects made donations to different charities. We found that the blood oxygenation level-dependent signal in ventral medial prefrontal cortex (VMPFC) correlated with the subjective value of voluntary donations. Furthermore, the region of the VMPFC identified showed considerable overlap with regions that have been shown to encode for the value of basic rewards at the time of choice, suggesting that it might serve as a common valuation system during decision making. In addition, functional connectivity analyses indicated that the value signal in VMPFC might integrate inputs from networks, including the anterior insula and posterior superior temporal cortex, that are thought to be involved in social cognition.

Introduction

There is a growing consensus in behavioral neuroscience and neuroeconomics that individuals make decisions by assigning values to different options and comparing them to make a choice (Montague and Berns, 2002; Wallis, 2007; Balleine et al., 2008; Rangel et al., 2008). Multiple studies have found evidence for such value signals at the time of choice in the ventral medial prefrontal cortex (VMPFC) in simple decisions involving primary or secondary rewards (Wallis and Miller, 2003; Padoa-Schioppa and Assad, 2006; Kable and Glimcher, 2007; Plassmann et al., 2007; Tom et al., 2007; Valentin et al., 2007; Wallis, 2007; Hare et al., 2008, 2009; Rolls et al., 2008). However, it is unknown whether the VMPFC also encodes the value of stimuli in more complex situations, such as those that arise in the social context, and what networks provide the input for these computations.

The current study addresses both questions using functional magnetic resonance imaging (fMRI) in a charitable giving task. Donations to charity represent a complex social decision in which the benefits for the giver are abstract and indirect, unlike decisions involving primary reward or money where the benefit is concrete. Although two previous neuroimaging studies of charitable giving (Moll et al., 2006; Harbaugh et al., 2007) have reported activity in regions that respond to primary reward, neither addressed the questions of what neural networks provide the input used to compute values. In the case of decisions over primary rewards (e.g., choosing which juice to drink), the value is likely to be influenced by sensory factors such as expected taste and by somatic states such as thirst. On the other hand, computing the value of a charitable donation might require inputs from areas involved in social cognition. For example, because giving to charity involves sacrificing resources for the benefit of others, these decisions are likely to require a shift in attention away from the subject's own state to focus on the needs of others. In addition, the value that we assign to addressing the needs of others might depend on how much empathy we feel for them.

We hypothesized that value signals in the VMPFC would reflect the integration of input from regions involved in social cognition, in particular the anterior insula and posterior superior temporal cortex (pSTC), during the charitable donation decisions. This hypothesis was based on previous neuroimaging studies suggesting that insula plays a role in empathy (Singer et al., 2004, 2006; Saarela et al., 2007), pSTC is involved in shifting attention to focus on another's perspective (Saxe and Kanwisher, 2003; Behrens et al., 2008; Hampton et al., 2008; Young and Saxe, 2009), and that both regions are related to altruistic behavior (Harbaugh et al., 2007; Tankersley et al., 2007).

Materials and Methods

Participants. Twenty-two subjects, all female, participated in this experiment (mean age = 24.7 years, range = 19–38 years). All subjects were right-handed, healthy, had normal or corrected-to-normal vision, had no history of psychiatric diagnoses, neurological or metabolic illnesses, and were not taking medications that interfere with the performance of fMRI. The review board of the California Institute of Technology (Pasadena, CA) approved the study.

Stimuli and task. Seventy-five charitable organizations were used in the study (supplemental Table S6, available at www.jneurosci.org as supplemental material). Before entering the scanner, subjects completed two self-paced computer tasks that presented images representative of each charity along with a one-paragraph description of its mission. In the first task subjects rated each charity for its deservingness (scale: −5 to 5). In the second task they rated each charity for its closeness to them (scale:

Received Aug. 19, 2009; revised Oct. 12, 2009; accepted Nov. 10, 2009.

We thank the Betty and Gordon Moore Foundation for their financial support, Hilke Plassmann for sharing the data used to construct Figure 6, and Cendri Hutcherson for valuable comments on this manuscript.

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DOI:10.1523/JNEUROSCI.4089-09.2010

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1–3), defined as the likelihood that the subject or someone they knew would directly benefit from its mission.

Before entering the scanner subjects received further instructions about the experiment. They were told that they had been endowed with $100 for participating in the experiment, and that whatever amount was not donated to the charity during the fMRI task was theirs to keep. Subjects knew that at the end of the experiment one of the trials would be randomly selected and implemented, and that the donation chosen in that trial was made anonymously to the charity. Note that, since only one trial was selected to count, subjects could treat each decision as being the only one, and did not have to worry about spreading their money across the different charities. In addition, subjects were informed that their donations to charity would be matched on a one-to-one basis by a separate pool of research funds. Thus, when a subject donated $25 from her endowment, the charity received $50. No deception was used in the experiment: all donations were made as described in the rules of the experiment.

After these instructions subjects completed 150 trials in the scanner. Each of the charities described in the prescan task was shown twice: once in a free donation trial and once in a forced donation trial. Figure 1 shows the timing of the trials. In free donation trials subjects indicated the amount they wished to donate to the charity ($0–$100). In forced donation trials subjects were instructed how much they had to donate in that trial. The amount required to be donated in each forced trial was randomly determined with replacement from a uniform distribution on $0 and $100 (in $5 increments). In both cases, subjects indicated the size of the donation using a button response pad that moved a cursor along a $0–$100 scale in $5 increments. The initial location of the cursor on the scale was determined randomly in both free and forced trials to prevent bias. The order of presentation of charities and conditions was randomized within and across subjects. Note that there was an equal probability that a free or a forced trial would be selected at the end of the experiment and implemented.

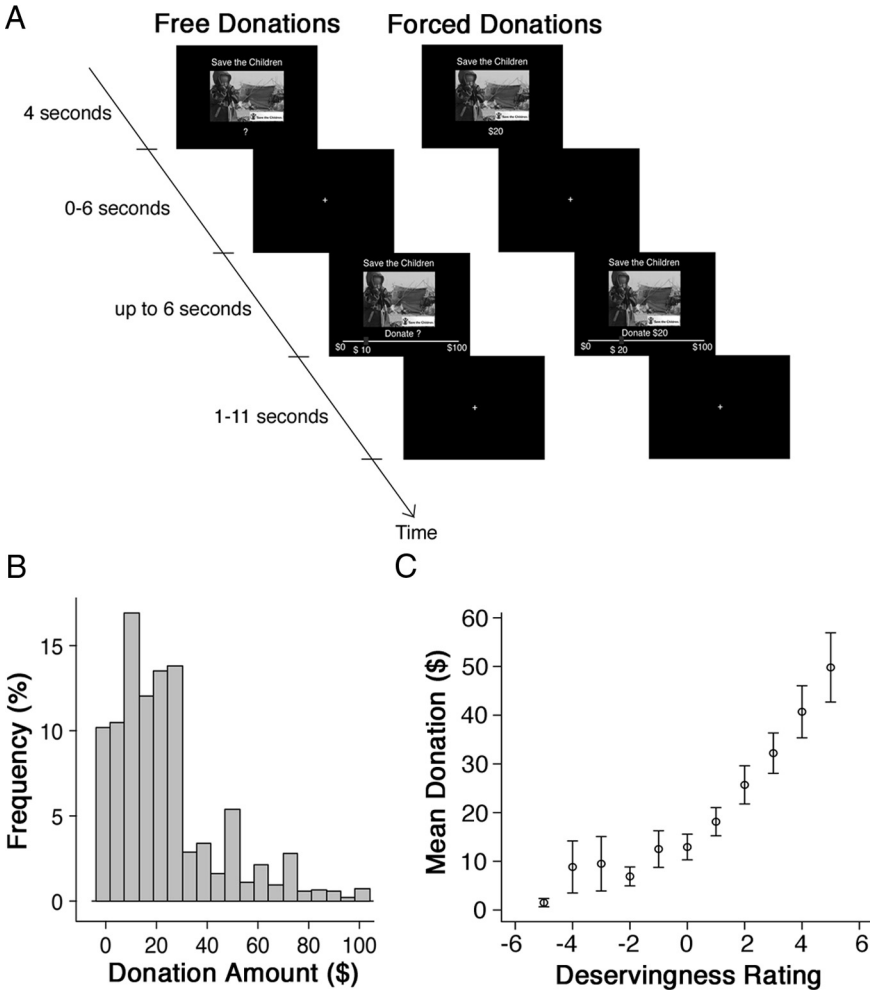

Figure 1. Experimental timeline and behavioral results. ***A***, The two trial types, free and forced donation trials, were identical except that in forced donation trials subjects were told the dollar amount that they had to donate to the charity. Each charity was presented twice, once as a free trial and once as a forced trial. Charity, trial type, and forced donation amount were fully randomized within subjects. ***B***, Frequency of donations in free trials for the entire group. ***C***, Donations as a function of deservingness ratings. Error bars represent the SEM.

Value of charitable donations. We used the amount donated to the charity in the free trials as our measure of the subjective value of making the optimal donation for a charity. We refer to this variable as DN. This is justified by the following standard economic model of charitable giving (Andreoni, 1990; Mas-Colell et al., 1995). Each trial subjects need to solve

$$\max_{d\in[0,100]} \theta\log(d) - d,$$

where d denotes the size of the donation, θ is a parameter measuring the quality or subjective value of the charity, and $\theta\log(d)$ is the amount of utility (measured in dollars) that the subject gets from donating $\$d$ to the charity. The optimal solution to this problem, denoted by d^*, is characterized by the following first-order-condition:

$$\frac{\theta}{d^*} = 1,$$

which implies that $d^* = \theta$. In other words, the optimal donation is proportional to the quality or subjective value of the charity, which justifies using donations as a measure of the subjective value of the charity. Note that for simplicity this derivation assumes a logarithmic functional form of donations. However, it can be easily shown that d^* and θ are highly correlated for any concave benefit function.

fMRI data acquisition. The functional imaging was conducted using a Siemens (Erlangen, Germany) 3.0 Tesla Trio MRI scanner to acquire gradient echo T2*-weighted echoplanar (EPI) images with blood oxygenation level-dependent (BOLD) contrast. To optimize functional sensitivity in the OFC, we used a tilted acquisition in an oblique orientation of 30° to the anterior commissure–posterior commissure line (Deichmann et al., 2003). In addition, we used an eight-channel phased array coil that yields a 40% signal increase in signal in the OFC over a standard head coil. Each volume comprised 32 axial slices collected in an interleaved-ascending manner. Data were collected in three sessions. The length of each session varied slightly and was on average 466 volumes (15.5 min). The imaging parameters were as follows: echo time, 30 ms; field of view, 192 mm; in-plane resolution and slice thickness, 3 mm; repetition time, 2 s. Whole-brain high-resolution T1-weighted structural scans ($1 \times 1 \times 1$ mm) were acquired from the 22 subjects and coregistered with their mean EPI images and averaged together to permit anatomical localization of the functional activations at the group level.

fMRI data preprocessing. Image analysis was performed using SPM5 (Wellcome Department of Imaging Neuroscience, Institute of Neurology, London, UK), except for the overlay image shown in Figure 2 that was created

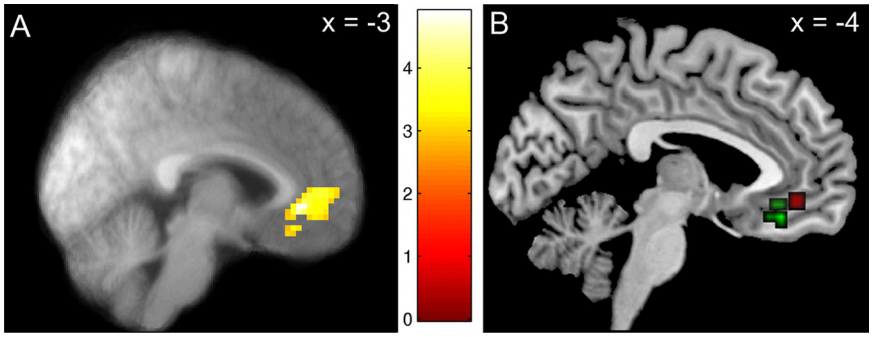

Figure 2. VMPFC activity correlated with the subjective value of charitable donations at the time of decision making. ***A***, Region of VMPFC in which activity correlates with the parametric modulator for the value of the charitable donations. Color scale denotes *Z*-scores. Statistical parametric maps are whole brain corrected for multiple comparisons at $p < 0.05$. ***B***, Overlay map showing the results of conjunction analyses identifying regions of VMPFC in which activity is correlated with the value of charitable donations in the current study, and with the value of primary rewards in other decision-making studies. Red, Conjunctions with value signals for primary food rewards described by Plassmann et al. (2007). Green, Conjunctions with value signals for primary food rewards described by Hare et al. (2008). Each contrast used in the conjunction analyses was thresholded at $p < 0.005$ unc.

using the MRIcron software (http://www.sph.sc.edu/comd/rorden/mricron/). Images were corrected for slice acquisition time within each volume, motion corrected with realignment to the last volume, spatially normalized to the standard Montreal Neurological Institute EPI template, and spatially smoothed using a Gaussian kernel with a full-width-at-half-maximum of 8 mm. Intensity normalization and high-pass temporal filtering (using a filter width of 128 s) were also applied to the data.

General linear model. We estimated a general linear model (GLM) in three steps. First, for each individual we estimated a GLM with first order autoregression and the following four regressors: (R1) picture presentation in free trials, (R2) picture presentation in forced trials, (R3) response in free trials, and (R4) response in forced trials. To take advantage of the parametric nature of our design, each of these regressors was modulated by the DN variable resulting in a total of 8 regressors of interest. In the case of forced trials DN represented the amount donated by the subject for the charity shown in the free donation condition. R1 and R2 were modeled as events with a 4 s duration. R3 and R4 were modeled as events with durations equal to the reaction time for that trial (as measured by the time elapsed between the appearance of the response screen and the first button press). The model also included session constants and motion parameters as regressors of no interest.

Second, we calculated the following first-level single-subject contrasts: C1, free donation trials at picture presentation modulated by DN; C2, forced donation trials at picture presentation modulated by DN; and C3, free trials modulated by DN minus forced trials modulated by DN at picture presentation; and C4, free minus forced trials at picture presentation unmodulated.

Third, we calculated second-level group contrasts using one-sample *t* tests on the single-subject contrasts. We performed whole brain corrections for multiple comparisons at the cluster level. For all of the main contrasts reported in the results section and figures, the individual voxel threshold was set to $p < 0.005$, and the extent threshold ranged from 95 to 120 voxels at a resolution of 3 mm^3, to achieve a corrected threshold of $p < 0.05$. The details of corrections for each contrast are listed in supplemental Tables S1–S5 (available at www.jneurosci.org as supplemental material). Anatomical localizations were performed by overlaying the *t*-maps on a normalized structural image averaged across subjects, and with reference to an anatomical atlas (Duvernoy, 1999).

Between-subjects correlates of giving. This analysis was performed in two steps. First, we constructed an individual specific measure of willingness-to-give using the following linear regression on each individual's decisions during the free trials:

$$\text{donation} = b_0 + b_1 * \text{deservingness} + b_2 * \text{closeness} + \text{error}.$$

Our measure of willingness-to-give (WTG) was given by the b_1 coefficient of the regression. Note that this coefficient is a better measure of overall willingness-to-give than just average donations because it controls for subject's views on the deservingness of the different charities (e.g., a generous individual might make small donations on average because she does not think highly of the charities that we used). The closeness measure was included in the regression to control for personal benefits derived from the charity's mission. Second, we performed a linear regression between the WTG measure and a measure of neural activity in pSTC for each subject given by the difference in the β values for the average BOLD responses in free minus forced trials. Figure 3*B* shows the relationship between both measures averaged over all of the voxels from the pSTC ROI shown in Figure 3*A*. Note that estimates for the b_1 coefficient were highly correlated across subjects ($r = 0.90$) when the regression was estimated using *z*-scores of the independent variables, which suggests that the measure of WTG was not sensitive to individual differences in the use of the ratings scales.

Psychophysiological interaction model 1. The purpose of this psychophysiological interaction (PPI) analysis was to identify regions exhibiting an increase in correlation with the VMPFC during the initial valuation phase in free and forced trials. It was performed in three steps.

First, for each individual we extracted the BOLD time-series from the voxel within a 4 mm sphere surrounding her activation peak within a mask of the VMPFC shown in Figure 2*A*. The individual peaks were identified using the contrast of the parametric regressor for DN in the free trials. Variance associated with the six motion regressors was removed from the extracted time-series. The time courses were then deconvolved based on the model for the canonical hemodynamic response to construct a time series of neural activity in the VMPFC following the procedures outlined in Gitelman et al. (2003).

Second, for every subject we estimated a GLM that included the following three regressors as well as motion parameters: (1) An interaction between neural activity in the VMPFC and the picture presentation time for all trials (free + forced) convolved with the canonical HRF; (2) A regressor specifying all trials as an indicator convolved with the canonical HRF; and (3) The original BOLD eigenvariate from the VMPFC (i.e., the first principal component of time-series from the voxels within the 4 mm sphere). Single subject contrasts were calculated following estimation of the GLM. (Note: see supplemental methods, available at www.jneurosci.org as supplemental material, for description of an extended version of PPI model 1.)

Finally, second level group contrasts were calculated based on the single subject contrast values using one-sample *t* tests. Figure 4*A* and supplemental Table S4 (available at www.jneurosci.org as supplemental material) report areas exhibiting a positive correlation with VMPFC, as captured by the significance of the first regressor of the GLM.

PPI model 2. The goal of this analysis was to identify regions showing an increase in correlation during the valuation period with pSTC and subsequently to determine whether there were regions showing PPI with both pSTC and VMPFC. The analysis proceeded in several steps. First, we computed a new PPI analysis that was identical to PPI model 1 except that it used activity in the pSTC ROI shown in Figure 3*A* rather than VMPFC as the source of the interaction. The individual peaks were identified using the interaction regressor from PPI model 1 (Similar results were obtained when the individual peaks were selected using the contrast of the parametric regressor for DN in the free trials from the primary GLM). Second, we performed a conjunction analysis to identify areas that exhibited a positive psychophysiological interaction with both pSTC and VMPFC using PPI models 1 and 2 at $p < 0.005$ uncorrected. The results are reported in Figure 4*B* and supplemental Table S5 (available at www.jneurosci.org as supplemental material).

PPI model 3. This analysis was conducted to determine whether VMPFC interactions with pSTC and anterior insula were specific to complex social decisions. We used a previously collected dataset in which the

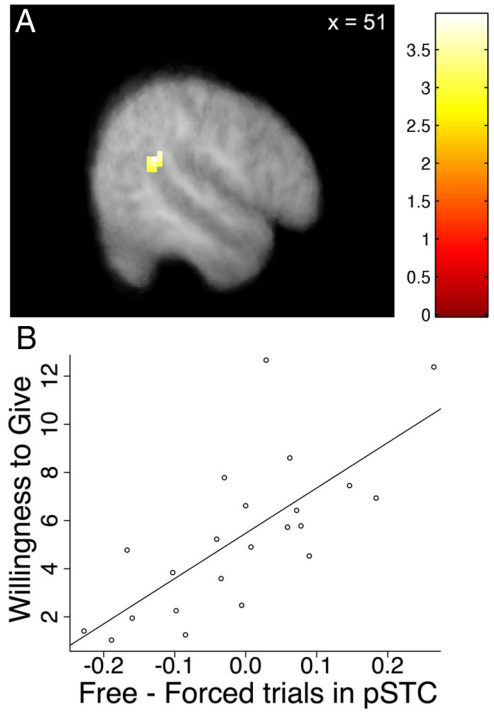

Figure 3. Activity in pSTC correlated with subjects' willingness-to-give. ***A***, Region of the right pSTC in which the difference in average activity between free and forced trials was was positively correlated with willingness-to-give. Statistical parametric maps are whole brain corrected for multiple comparisons at $p < 0.05$. Color scale denotes *Z*-scores. ***B***, Scatter plot showing the correlation between a behavioral measure of overall willingness-to-give and average activity in the area of pSTC showed in Figure 3*A*. The scatter plot is for the purpose of display only and was not the basis of any inferences in this study. Each point represents one subject.

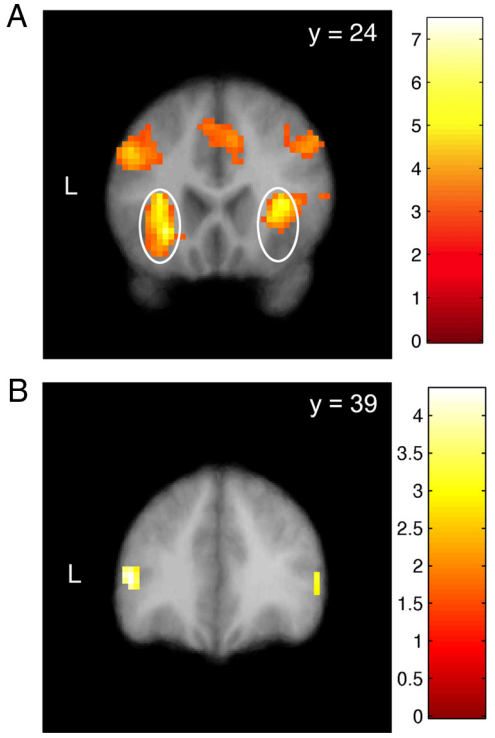

Figure 4. Regions exhibiting PPI with VMPFC during all trials. ***A***, Regions exhibiting an increased correlation with VMPFC activity during the charity evaluation period at $p < 0.05$ corrected. The anterior insula is circled in white. ***B***, Conjunction analysis showing areas of IFG that exhibit functional connectivity with both pSTC and VMPFC during the decision period. A threshold of $p < 0.005$ uncorrected was used for the conjunction. Color scale denotes *Z*-scores.

experimental design was identical to the current study except that subjects made decisions about paying money for primary rewards (snack foods) for themselves rather than decisions about giving to charity (Plassmann et al., 2007). Data were only available for 18 of the originally reported 19 subjects due to technical difficulties retrieving the stored data. This PPI model was identical to PPI model 1 except that the seed regions in VMPFC were selected from a mask given by the conjunction of voxels that correlated with DN in the current study and with willingness-to-pay (WTP; a measure of subjective value) in the food reward study, both at $p < 0.005$ uncorrected. The individual subject peaks were selected using the contrast for WTP in the free trials from the food reward task.

Two-sample one-tailed *t* tests were used to test whether the VMPFC psychophysiological interactions were stronger in the anterior insula and pSTC during charitable donation decisions than food reward decisions. Averaged PPI coefficients were extracted for each subject from ROIs in pSTC, anterior insula, and IFG. The pSTC ROI contained all voxels showing a significant between-subjects correlation with WTG at $p < 0.001$ uncorrected. The anterior insula ROI contained all voxels that were more active in the free versus the forced donation conditions at $p < 0.001$ uncorrected for the right insula and $p < 0.0001$ uncorrected for the left insula. A higher threshold was used in the left insula to restrict the ROI to the desired anatomical structure. The bilateral IFG ROI contained all voxels showing a significant interaction with VMPFC in both the donation and food purchasing decision tasks (conjunction threshold $p < 0.05$ uncorrected).

PPI model 4. This analysis was conducted to determine whether pSTC interactions with IFG were greater during charitable donation than food reward decisions. This model is identical to PPI model 2 except that it was conducted on the data from Plassmann et al. (2007). The individual subject peaks were selected using the contrast for WTP in the free trials from the food reward task. Two-sample one-tailed *t* tests were used to test whether the psychophysiological interactions were stronger between pSTC and IFG during charitable donation decisions than food reward decisions. The comparison of PPIs was based on the IFG conjunction between donation and food purchase conditions described in PPI model 3.

Mediation analysis. We performed a mediation analysis to test whether the interaction between pSTC and VMPFC was mediated by the IFG using the software described by Wager et al. (2008) and graciously made freely available at http://www.columbia.edu/cu/psychology/tor/. Briefly, this analysis was based on a standard three-variable path model as shown in Figure 5 (Baron and Kenny, 1986). Following convention, we required that three tests reach statistical significance in the mediation analysis. First the initial variable must be related to the mediating IFG variable (Fig. 5, Path *a*). Second, the mediating variable must be related to the outcome variable after controlling for the initial variable (Fig. 5, Path *b*). Third, the mediation effect defined as product of the indirect paths (*a***b*) must be significant. This third criterion tests that including the mediator in the path model significantly reduces the predictor-outcome relationship. Statistical significance was determined using bootstrap tests with 100,000 iterations. The initial variable (pSTC) was the interaction term between pSTC activity and the picture presentation in all trials (identical to the interaction regressor for PPI model 2). The mediating variable (IFG) was the interaction term between IFG activity and the picture presentation in all trials (identical to the interaction regressor for PPI model 4). The outcome variable (VMPFC) was the interaction term between VMPFC activity and the picture presentation in all trials (identical to the interaction regressor for PPI model 1).

Results

Behavioral

The task was divided into two trial types: (1) free donation trials, and (2) forced donation trials (Fig. 1*A*). In free trials subjects decided how much of their endowment ($0–$100) to donate to the charity shown on the current trial. In forced trials, subjects were required to donate an amount between $0 and $100 that was

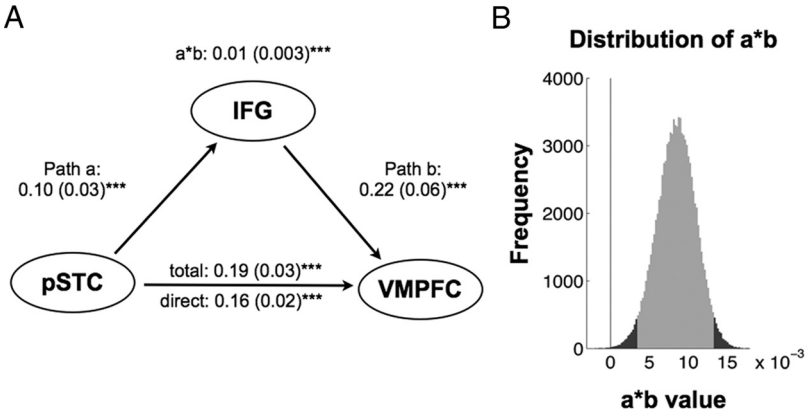

Figure 5. Results of the mediation analysis testing the relationship between pSTC, IFG, and VMPFC activity. ***A***, Diagram of the path model showing the coefficients ± SEM, significant at ***$p < 0.001$. ***B***, Histogram of the bootstrapped distribution of the mediation effect (*a*b*). The lighter gray color denotes the 95% confidence interval.

randomly selected by the computer. Figure 1*B* shows the distribution of donations in the free trials. Subjects chose to donate at least $5 in 90% of the free trials. Subjects also rated the deservingness of each charity outside the scanner and the amount donated to a charity increased with its deservingness rating (Fig. 1*C*).

fMRI

Neural correlates of the value of donations

We conducted a whole brain analysis to look for regions in which activity correlated with the subjective value of donations during the free trials. As described in the methods section, the amount of money donated to a charity during the free trials (DN) is a valid behavioral measure of the subjective value of making an optimal donation to that charity. Only the VMPFC, encompassing ventral anterior cingulate and the medial orbitofrontal cortex, was significantly correlated with subjective value during free trials after correcting for multiple comparisons ($x, y, z = -3, 39, -3$; $p < 0.05$ corrected) (Fig. 2*A*). For completeness, all regions showing a correlation at $p < 0.005$ uncorrected are listed in supplemental Table S1 (available at www.jneurosci.org as supplemental material). No areas exhibited a similar correlation during the forced trials at $p < 0.05$ after whole brain or small volume corrections. However, a direct comparison between the correlation with DN in free and forced trials showed no significant difference between the two conditions at corrected thresholds. A contrast of average activity in free and forced trials showed that several regions including the VMPFC ($x, y, z = -12, 42, -15$) and striatum ($x, y, z = 15, 18, 0$) were more active in free donation trials ($p < 0.05$ corrected; supplemental Table S2, available at www.jneurosci.org as supplemental material).

Overlap with value signals in basic rewards paradigms

We investigated this issue further by carrying out a conjunction analysis with two previous studies from our group that had identified correlations between VMPFC activity and subjective valuation of primary rewards at the time of choice (Plassmann et al., 2007; Hare et al., 2008). Figure 2*B* plots areas in which activity correlated with the value for charitable donations in the current study and with the value of primary rewards in previous studies.

Neural correlates of average willingness-to-give

We also tested for regions whose activity was correlated with the average level of giving for different subjects. We constructed an individual measure of the willingness-to-give for each subject (see methods for details). We then performed a linear regression at the second level to identify areas in which willingness-to-give was correlated with the contrast of free minus forced donation trials. Note that this contrast provides a measure of the average increase in activity during free trials relative to the forced trial baseline. Activity in the right pSTC was positively correlated with willingness-to-give ($x, y, z = 51, -45, 21$; $p < 0.05$ corrected) (Fig. 3; supplemental Table S3, available at www.jneurosci.org as supplemental material).

Neural systems interacting with the VMPFC during value computations

We tested the hypothesis about the role of inputs from regions involved in social cognition to the value computations of VMPFC by carrying out a series of psychophysiological interaction (PPI) analyses. These PPI analyses were designed to test three questions: (1) Are there interactions between VMPFC and regions previously implicated in social cognition during charitable donation decisions? (2) Do regions involved in social cognition interact with networks that provide input to VMPFC thereby influencing value computations indirectly? (3) Are these interactions stronger in the case of charitable donations than in decisions about obtaining primary rewards for oneself?

The first PPI analysis was designed to identify regions that interacted with the VMPFC during the valuation period of all trials (free or forced). A whole brain analysis showed that activity in several regions including the bilateral anterior insula ($x, y, z = -27, 24, -6$ and $33, 24, 9$; $p < 0.05$ corrected) interacted positively with the VMPFC (Fig. 4*A*; supplemental Table S4, available at www.jneurosci.org as supplemental material). Although the connectivity between pSTC and VMPFC did not survive whole brain correction, there were voxels in pSTC that showed an interaction with VMPFC at $p < 0.005$ uncorrected. Moreover, there was an overlap between voxels in the pSTC that correlated with willingness-to-give across subjects and those that showed positive PPI with the VMPFC (supplemental Fig. S2, available at www.jneurosci.org as supplemental material).

Because the interaction between VMPFC and pSTC was less robust than the interaction between the insula and VMPFC, we hypothesized that pSTC and VMPFC may interact indirectly as postulated in our second question above. We explored this hypothesis in two steps. First, we estimated a second PPI model designed to identify regions exhibiting positive functional connectivity with the pSTC during the valuation period. This analysis showed a positive PPI between pSTC and the inferior frontal gyrus (IFG; $x, y, z = -45, 42, 6$; $p < 0.05$ corrected; supplemental Table S5, available at www.jneurosci.org as supplemental material), a region previously shown to link activity in cortical regions with VMPFC (Hare et al., 2009). A conjunction of the results from both PPI analyses showed that pSTC and VMPFC have joint positive functional connectivity with the IFG bilaterally ($x, y, z = -45, 39, 6$ and $51, 45, 0$; conjunction threshold $p < 0.005$ uncorrected with 5 contiguous voxels) (Fig. 4*B*). Second, we conducted a mediation analysis to test whether the IFG might mediate the interaction between pSTC and VMPFC. Figure 5 shows the results

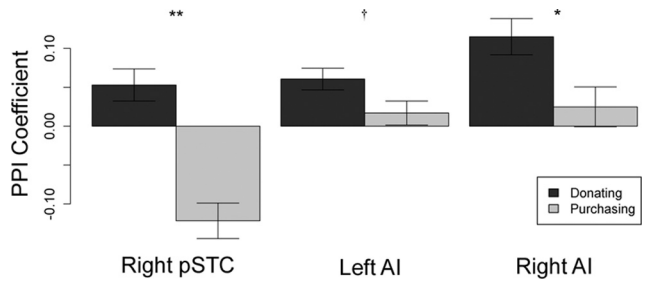

Figure 6. Differences in VMPFC task related connectivity during charitable donation and food reward decisions. Dark gray bars represent mean ± SEM of the VMPFC PPI coefficients in right pSTC and both the left and right anterior insula (AI). Light gray bars represent the VMPFC PPI coefficients for the same regions during decisions about purchasing a snack food item for oneself in a separate study (Plassmann et al., 2007). Regions where the difference in PPI between decision tasks is significant are indicated as $^{*}p < 0.05$, $^{**}p < 0.005$, and $^{\dagger}p < 0.1$. PPI coefficients are not significantly different from zero during the food decision task in any of the three regions.

of this analysis and suggests that IFG is a partial mediator of the interaction between pSTC and VMPFC.

Finally, we tested whether the VMPFC-anterior insula, VMPFC-pSTC, VMPFC-IFG, and pSTC-IFG interactions were stronger during donation decisions than decisions about primary rewards. To do so we used data from a previously published study that used a similar experimental design in which subjects made decisions about food items rather than charities (Plassmann et al., 2007). We compared the PPI coefficients between VMPFC, pSTC, and the anterior insula during charitable donations to food decisions using one-tailed, two sample *t* tests. There was a stronger interaction between VMPFC and the right pSTC ($t_{(38)} = 2.92$, $p < 0.005$), and right anterior insula ($t_{(38)} = 1.83$, $p < 0.05$) during charitable donation than food decisions (Fig. 6). There was greater PPI between the VMPFC and left anterior insula in the donation decisions compared with the food purchase task at the level of a trend ($t_{(38)} = 1.51$, $p < 0.07$). There was no difference in PPI between VMPFC and IFG in the two conditions ($t_{(38)} = 0.64$, ns). There was a stronger interaction between the pSTC and IFG during charitable donation than food decisions ($t_{(38)} = 4.15$, $p < 0.0001$).

Discussion

Our results show that the value of a charitable donation is reflected in VMPFC activity. Furthermore, the area of VMPFC involved in computing the value of charitable donations is in close proximity to regions that have been shown in previous studies to encode the value of primary and secondary rewards at the time of decision making (Wallis and Miller, 2003; Padoa-Schioppa and Assad, 2006; Kable and Glimcher, 2007; Plassmann et al., 2007; Tom et al., 2007; Valentin et al., 2007; Hare et al., 2008, 2009; Rolls et al., 2008). This provides support for the hypothesis that the VMPFC encodes value signals for a wide range of stimuli, from primary to complex and abstract. Using the same circuitry to encode the value of very different stimuli would be useful in decisions that involve the comparison of different types of stimuli, such as charitable donation decisions which involve both money and the charitable work (Montague and Berns, 2002).

The PPI results are consistent with the hypothesis that value signals in VMPFC might be computed on the basis of input from regions involved in social cognition, specifically anterior insula and pSTC. The finding that there are stronger interactions between these two regions and VMPFC valuation systems in the context of charitable donations than in decisions about food rewards suggests a specific interaction between social cognition networks and value computation systems during complex social decisions. These two areas have been previously shown to be involved in aspects of social cognition. In particular, previous work has suggested that the anterior insula is involved in empathy (Singer et al., 2004, 2006; Saarela et al., 2007) and the pSTC may signal shifts in the focus of attention in both social and non-social contexts (Saxe and Kanwisher, 2003; Frith and Frith, 2006; Behrens et al., 2008; Hampton et al., 2008; Mitchell, 2008; Young and Saxe, 2009). It is important to emphasize, however, that while our data on local activity and PPI are consistent with the hypothesis that insula and pSTC influence value computations in VMPFC, they cannot establish the directionality or causality of the relationship between these areas.

Decisions to give money to a charity may require the giver to focus on the needs of others rather than or in addition to herself. Posterior STC has been implicated in the perception of agency or intent in the actions of other people as well as inanimate objects (Saxe and Kanwisher, 2003; Frith and Frith, 2006; Young and Saxe, 2009). In addition, the pSTC has been shown to reflect an updating signal in decision contexts where the optimal choice depends on predicting the intentions of another person (Behrens et al., 2008; Hampton et al., 2008). However, it has been suggested that pSTC functions are not specific to social cognition, but instead play a more general role in shifting attention in both social and non-social contexts (Mitchell, 2008). Together these data lead us to speculate that the pSTC might contribute to the computation of charities' values by shifting attention away from the self to focus on the needs of others.

Activity in pSTC may modulate the inputs to VMPFC during charitable donation decisions. The region of IFG that appears to link activity in pSTC with the VMPFC has been shown to correlate with subjective values during decisions about obtaining primary rewards (Plassmann et al., 2007; Hare et al., 2008). Anatomical connections between these three regions are supported by data from nonhuman primates (Barbas and Pandya, 1989; Hackett et al., 1999; Romanski et al., 1999) and the data from these tracer studies are consistent with the direction of influence assumed in our mediation analysis. PPI analyses from a previous decision-making study (Hare et al., 2009) also suggest that this IFG region may provide input to the VMPFC that is used in the computation of value for primary rewards. On the basis of these previous findings, as well as the fact that the connectivity between IFG and VMPFC did not differ in charitable donations compared with food decisions in the current study, we hypothesize that IFG may serve as a general input region to VMPFC during value computation. The correlation between willingness to give and activity in the pSTC together with the pSTC-IFG connectivity suggests that the pSTC may influence the degree to which IFG activity reflects aspects of the needs of others compared with self-relevant factors.

Deciding how much to donate requires not only attending to the needs of others, but also empathizing with those needs. Empathic concern for others in pain has been associated with activity in the anterior insula (Singer et al., 2004, 2006; Saarela et al., 2007) suggesting that it may be one source of empathy related input during value computation. Furthermore, there are known anatomical connections between the insula and VMPFC (Ongur and Price, 2000) and we found evidence that portions of the insula similar to those implicated in empathy for pain had task related increases in functional connectivity with the VMPFC. These findings lead us to speculate that information about the

states and feelings of others may be used by the VMPFC during the computation of the values for charitable donations.

Two previous studies of charitable decision making (Moll et al., 2006; Harbaugh et al., 2007) reported activity in networks that respond to primary rewards. An important difference with these previous studies is that our PPI analyses allow us to characterize the networks that inform value computations during charitable giving. Nevertheless, in terms of local activity, our results are largely consistent with these previous studies. Moll et al. found that activity in the VMPFC increased when donating to charities. This is consistent with our results because subjects are more likely to give to a charity that has high value for them. Similarly, Harbaugh et al. showed that reward related regions in the striatum and insula were more active during free than forced donation trials, again consistent with our data. Harbaugh et al. also showed that activity in the reward networks correlated with donation amount in the absence of choice, which is consistent with our findings that there are weak/noisy correlations between VMPFC activity and value in forced trials. Together these data suggest that signals related to value, although not necessarily explicit value computations, are present in the absence of the requirement for choice. Further elucidation of these value related signals outside of the time of choice will be an important aspect of future research.

There is one inconsistency between our findings and the previous studies mentioned above. Moll et al. reported a positive correlation between activity in the striatum/septum and the frequency of donation across subjects, and Harbaugh et al. reported a similar correlation with activity averaged across the caudate, nucleus accumbens, and insula. In contrast, while we did find greater striatal activity in free than forced trials, we did not find any correlations between striatal activity and subjective value, donation frequency, or willingness to give (see supplemental Tables S1 and S3, available at www.jneurosci.org as supplemental material). One important design difference between our study and theirs might account for the inconsistency. The correlation with donation frequency in Harbaugh et al. is with the contrast of money given to the charity minus monetary gain for the subject. The paradigm in Moll et al. also included trials where the subjects gained money, while our task did not. The relationship between reward signals in the striatum in response to gains for self versus others and charitable giving is an avenue for future research. Reassuringly, we did find that activity in pSTC was related to individual differences in charitable giving. Previous work has shown that there is a correlation between activity in pSTC and self-reported altruism (Tankersley et al., 2007). Our findings confirm and extend this result by showing that activity in this area is correlated with subjects' actual willingness to give in real decisions. Furthermore, our connectivity analyses suggest a functional pathway through which pSTC can influence value computations during charitable giving.

Our results have applications to models of the psychology and economics of giving. One basic hypothesis that has been proposed in behavioral economics is that the amount given to a charity depends solely on the giver's preferences for that donation (Andreoni, 1990; Fehr and Schmidt, 1999; Fehr and Camerer, 2007). The functional connectivity data presented here suggest that social cognition capabilities might also play a role in determining the size of the donation, perhaps by influencing how the value of giving (i.e., the preferences) are computed at the time of the decision. For example, a subject who does not activate the insula might end up giving a small donation because she does not generate the empathy necessary to construct such a preference. Similarly, a subject who does not activate pSTC with sufficient strength might make a small donation (as shown in Fig. 4), not because she is indifferent to the charity's beneficiaries when she is able to take their perspective, but because she has difficulty focusing her attention on others. In the future, additional tests of this model could be conducted using temporary inhibition techniques like rTMS or using individual differences in empathic concern.

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